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The most frog-diverse place in Middle America, with notes on the conservation status of eight threatened species of amphibians

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***Abstract.*—Regarding amphibians, Costa Rica exhibits the greatest species richness per unit area in Middle America, with a total of 215 species reported to date. However, this number is likely an underestimate due to the presence of many unexplored areas that are difficult to access. Between 2012 and 2017, a monitoring survey of amphibians was conducted in the Central Caribbean of Costa Rica, on the northern edge of the Matama mountains in the Talamanca mountain range, to study the distribution patterns and natural history of species across this region, particularly those considered as endangered by the International Union for Conservation of Nature. The results show the highest amphibian species richness among Middle America lowland evergreen forests, with a notable anuran representation of 64 species. The greatest diversity in the study area occurred in the mature forest on the basal belt. Of the 68 amphibian species found, seven (10%) are endemic to the Atlantic versant and eight (11.6%) are threatened. This survey includes the first record of *Gastrotheca cornuta* in Costa Rica since it was last reported 21 years ago. New populations of *Agalychnis lemur* (Critically Endangered) and *Duellmanohyla uranochroa* (Endangered) are reported, and *Ecnomiohyla veraguensis* (Endangered) is reported for the first time in Costa Rica. These findings show that this locality is a high priority conservation area for a large number of amphibian species, which are often threatened by habitat loss and fragmentation.**

Keywords. Biodiversity, Costa Rica, Endangered, Limón province, patterns of distribution, Tropical Wet Forest

***Resumen.*—En anfibios, Costa Rica exhibe la mayor riqueza de especies por unidad de área en América Meridional con un total 215 especies documentadas a la fecha. Sin embargo, es probable que este número esté subestimado debido a la presencia de áreas inexploradas con difícil acceso. Entre 2012 y 2017, realizamos un monitoreo de anfibios en el Caribe Central de Costa Rica, en el borde norte de la Fila Matama en la Cordillera de Talamanca, para estudiar los patrones de distribución y la historia natural de las especies en esta región, particularmente aquellas consideradas en peligro por la Unión Internacional para la Conservación de la Naturaleza (UICN). Nuestros resultados muestran la mayor riqueza de especies de anfibios en los bosques perennes de tierras bajas de América Meridional, con una notable representación de anuros de 64 especies. La mayor diversidad en el área de estudio se encontró en el bosque maduro en el piso basal. Del total de especies, siete (10%) son endémicas de la vertiente Atlántico y ocho (11,6%) están amenazadas. Este es el primer registro de *Gastrotheca cornuta* en Costa Rica después de 21 años desde que se registró por última vez. Descubrimos nuevas poblaciones de *Agalychnis lemur* (en Peligro Crítico), *Duellmanohyla uranochroa* (en Peligro), y reportamos por primera vez *Ecnomiohyla veraguensis* (en Peligro) en Costa Rica. Nuestros resultados muestran que esta localidad es un área de alta prioridad para la conservación de una gran cantidad de especies de anfibios, a menudo amenazadas por la fragmentación y la pérdida de hábitat.**

Palabras clave. Biodiversidad, Costa Rica, amenazado, provincia de Limón, patrones de distribución, Bosque Tropical Húmedo

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Introduction

Currently, more than 8,000 species of amphibians have been described worldwide, with the greatest diversity occurring in the Neotropics (Duellman 1999a; Frost 2019), where lower Central America stands out as a region with a substantial number of species (Campbell 1999; Duellman 2001; Savage 2002; Kubicki 2007). However, there has been an increase in the numbers of species designated as endangered throughout this region since the late 1980s due to habitat deforestation (Young et al. 2001; Stuart et al. 2004; Becker et al. 2007), climate change (Pounds et al. 1999; Hof et al. 2011), and infectious diseases (Lips et al. 2003; Pounds et al. 2006; Wake and Vredenburg 2008).

Tropical forests harbor a considerable number of amphibian species across distinct microhabitats that are often related to water-dependent sites such as ponds, temporary swamps, streams, tree holes, and bromeliad axils (Duellman 1970; Savage 2002; Lehtinen et al. 2004; Haddad and Prado 2005). However, many other amphibians exhibit reproductive modes that are totally independent from water bodies (Savage 2002). For instance, frogs of the genera *Gastrotheca* (Hemiphractidae), *Eleutherodactylus* (Eleutherodactylidae), *Incilius* (formerly *Crepidophryne*: Bufonidae), *Craugastor, Pristimantis,* and *Strabomantis* (Craugastoridae) lay encapsulated eggs out of water, in which embryos undergo direct development and hatch out as small adults (Savage 2002; Gray and Bland 2016).

Costa Rica is known to possess considerable amphibian species richness per unit area (Savage 2002; Sasa et al. 2010; Bolaños et al. 2011). However, this great richness is likely to be underestimated due to the presence of undiscovered and undescribed species in areas that tend to be not easily accessible. To date, several previous works have reported countrywide amphibian checklists (Savage 2002; Bolaños et al. 2011; Leenders 2016). In particular, an increasing interest has focused on documenting species occurrence and the population status of threatened species in Costa Rica's montane ecosystems (Hayes et al. 1989; Abarca 2012; Acosta-Chaves et al. 2015; Rovito et al. 2015) and tropical forests of varying altitudinal gradients in the Pacific Slope throughout its South (McDiarmid and Savage 2005), Central (Laurencio and Malone 2009), and Northern regions (Sasa and Solorzano 1995). In contrast, the amphibian diversity of the Costa Rican Atlantic has been broadly documented almost exclusively in its Northern region (Donnelly and Guyer 1994; Guyer and Donnelly 2005; Whitfield et al. 2007). Only recently, Kubicki (2008) compiled the first list of species in premontane moist forests of the Costa Rican central-Caribbean. Although that inventory showed the relevant diversity of amphibians, little is known about the current population status and distribution of amphibian species across other areas of the mid-Caribbean.

Along this region, the Talamanca mountain range stands out as a predicted high priority conservation area for amphibians (García-Rodríguez et al. 2011). Considering that long-term monitoring can accurately assess population conditions (La Marca et al. 2005), species inventories are key to covering gaps in the distribution and natural history of endangered species in order to determine appropriate conservation strategies (Peloso 2010; Verdade et al. 2012). This study assessed the local richness and species distribution of amphibians in Veragua Rainforest Eco Research and Adventure Park and its surroundings on the northern edge of the Matama mountains in the Talamanca mountain range. Diversity analysis was conducted for different types of altitudinal belts, forests, and microhabitats found across the sampling area, and the population status of the threatened species in the study area are discussed.

Materials and Methods

Study area. The study was conducted in the Central Caribbean of Costa Rica between Las Brisas de Veragua town (9°57'07"N, 83°12'11"E; 233 m asl) and Plátano peak (9°51'50"N, 83°14'10"E; 1,000 m asl) on the northern edge of the Matama mountains in the Talamanca mountain range, including Chimú peak (9°52'48"N, 83°14'13"E; 741 m asl) and Veragua Rainforest Park (VRP; 9°55'30"N, 83°11'28"E; 420 m asl; Fig. 1). This private reserve covers 3,200 ha of protected land ranging from 200–420 m asl, and it comprises mature forest, secondary vegetation at different stages of regeneration, open areas, and dirt roads. The study site lies adjacent to Victoria (9°55'21.73"N, 83°10'2.43"E; 410 m asl) on the Victoria river basin and the Matama mountains. This area is the closest point of the Talamanca mountain range to the Caribbean Sea and it forms part of the buffer zones of La Amistad International Park (an UNESCO World Heritage Site), the Banano river basin protected area, and the influence zones of the Zent, Peje, and Chirripó rivers, as well as the Bajo Chirripó indigenous reserve (SINAC 2018). Sampling was carried out along the elevation range 200–1,000 m asl, where two types of forest are located according to Holdridge (1967): Basal Tropical Wet Forest (200–600 m asl) and Premontane Tropical Wet Forest (601–1,000 m asl). Only these altitudinal belts are recorded and reported here, because they both represent the Tropical Wet Forest.

Data collection. Data were collected between January 2012 and December 2017. To record the species richness, samplings were standardized through diurnal and nocturnal visual and acoustic recognition searches (Crump and Scott 1994) into three transects: two in VRP, covering approximately 4 km each (Transects A and B), and one carried out along an 11 km trail between the reserve and Plátano peak (Transect C), including Chimú peak halfway along the route. On each of these

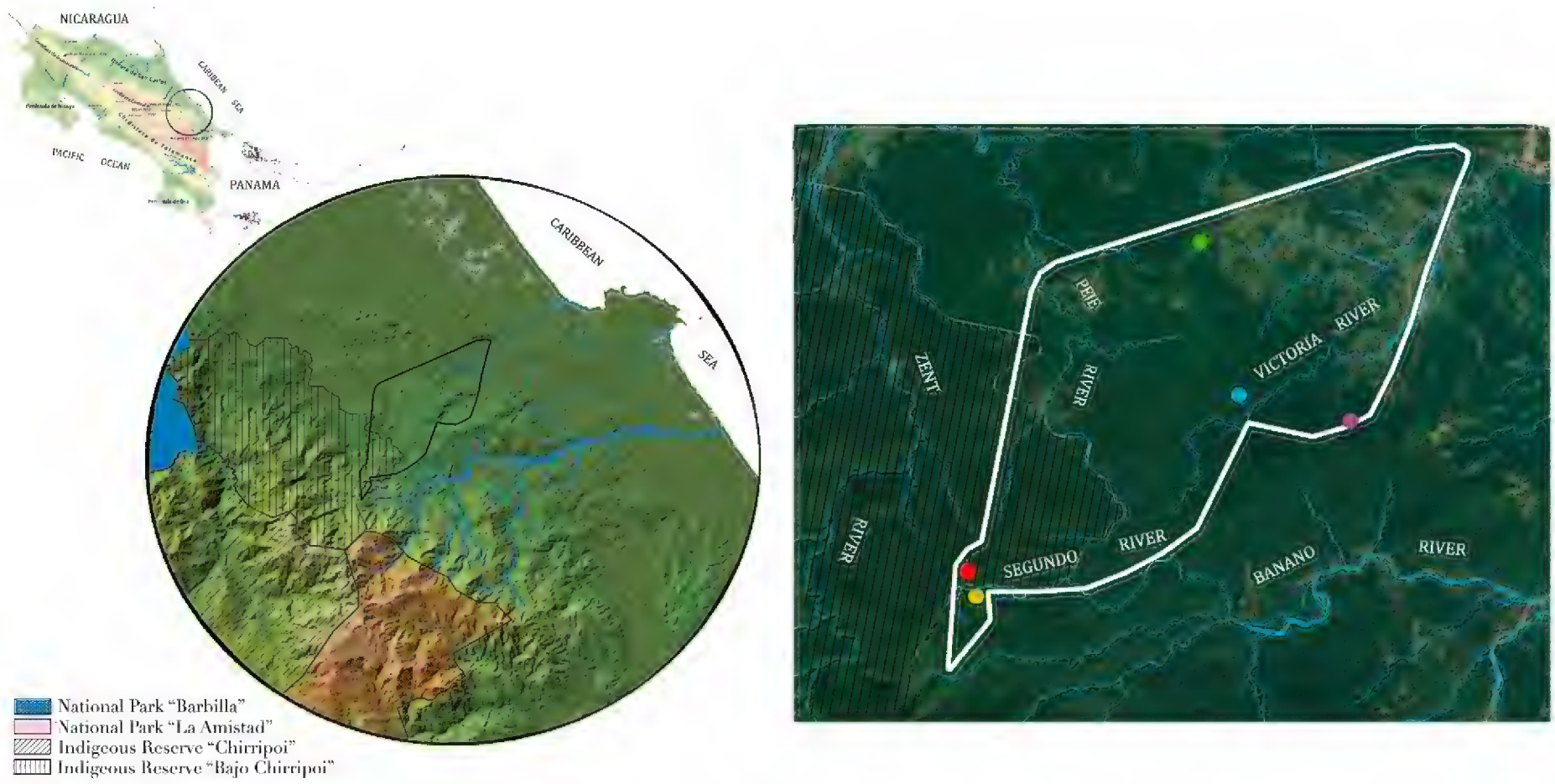

Fig. 1. Location of the study area (51 km^2) in the Limón Province in the Central Caribbean area of Costa Rica. The colored points represent the main localities of the study area: yellow (Chimú Peak), red (Plátano Peak), blue (Veragua Rainforest Research and Adventure Park), green (Las Brisas), and purple (Victoria).

transects, surveyors walked side-by-side at a constant speed to record amphibian diversity on both sides of the trail (Seber 1986), covering up to 10 m from each side towards the forest. Transect A (300–420 m asl) was located along a dirt road inside the reserve in a secondary forest edge that included a 30 m wide natural pond and open areas. Transect B (200–400 m asl) covered forest trails and riparian environments within a mature forest. Transect C (400–1,000 m asl) comprised an old wood road (4 km) in a secondary forest and an indigenous trail (7 km) within a pristine environment that included natural ponds and riparian habitats along the trail.

From January 2012 to December 2012, Transect A or B was sampled weekly during the day (6:00–11:00 h) and at night (18:00–22:00 h), totaling 27 field days with four person hours (ph) per transect for a total search effort of 1,728 ph. Once a year, between 2012 and 2017, six expeditions at Transect C were conducted, totaling 13 field days of diurnal and nocturnal monitoring and a search effort of 1,560 ph. A leaf litter plot survey (Scott 1976) was used to sample ten plots (8 x 8 m) in Chimú peak (2014, 2017) and Plátano peak (2013, 2015) on an annual basis, for a total of 40 sampled plots.

The following information was recorded for the species detected during monitoring: 1. Holdridge altitudinal belts: basal (b) or premontane (p); 2. Type of forest: mature (M) or disturbed (D; includes secondary forest and open areas), and 3. Habitat association: riparian (R), forest (F), or swamp (S; including temporary or permanent ponds). If possible, one specimen per species was collected on each Holdridge life zone. The collected specimens were anesthetized and euthanized with lidocaine, fixed in a 10% buffered formalin solution, and later preserved in 70% ethanol solution. For all specimens, tissue samples of muscle and liver were collected and fixed in 95% ethanol. Voucher specimens and tissue samples were deposited at the Museo de Zoología of the Universidad de Costa Rica (UCR). Some specimens were collected by third parties or other VRP researchers through occasional encounters in random field trips.

The species list includes the information obtained from this monitoring effort and UCR records of the Victoria locality, covering a study area of 51 km^2, hereafter referred to as Veragua. Additional photographic material from collaborations with specialists in this area was evaluated. The taxonomic nomenclature follows Frost (2019), except for hylids in which Faivovich et al. (2018) was followed. The conservation status of each species was categorized according to the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN 2019) and registered observations on the natural history of threatened species.

Data analysis and permission. The Jaccard index (I_j) was used to determine the similarity in species composition between altitudinal belts, forest types, and habitat association. A species accumulation curve was performed to account for species richness. Sampling was conducted under research permit SINAC-ACLAC-PIME-VS-R-024-2016, granted by Sistema Nacional de Areas de Conservación (National System of Conservation Areas, SINAC).

Results

Overall Results

The surveys recorded a total of 68 species of amphibians, including 64 anurans distributed in 11

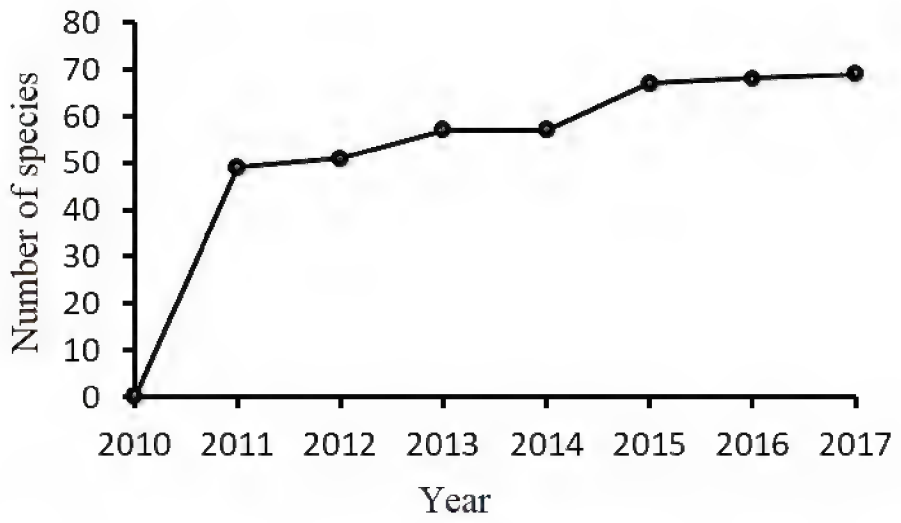

Fig. 2. Amphibian species accumulation curve for the 2010–2017 period in the study area.

families and 31 genera, three salamanders of the family Plethodontidae in two genera, and one caecilian in the family Caeciliidae (Table 1; Plates I–V). The most speciose families were Hylidae with 22 species (32.4%), followed by Craugastoridae with 15 species (21.7%) and Centrolenidae with 10 species (14.5%) [Table 1]. Six of the 68 species (8.7%) were endemic to the Atlantic slope of Costa Rica: *Bolitoglossa alvaradoi*, *Oedipina berlini*, *Craugastor persimilis*, *Diasporus amirae*, *Hyalinobatrachium dianae,* and *Ecnomiohyla sukia*. The species accumulation curve reached an asymptotic phase at the end of the sampling period (Fig. 2).

Low species similarity was obtained between basal and premontane belts (I_j = 0.37) and the majority of premontane species were found in the basal belt, except for *C. persimilis*, *D. amirae*, and *Pristimantis caryophyllaceus* (Table 1; Fig. 3a). Mature forests and disturbed areas were found to share slightly more than half of the species (I_j = 0.52). A total of 19 species were only present in mature forests, and 14 species were detected only in disturbed areas (Table 1; Fig. 3b). The most diverse habitats were the forest (43 sp.) and riparian (31 sp.) environments, while 20 species were associated with swamps (Fig. 3c; Table 1). The results show that 44 species were only found in one type of habitat; out of these, the forest (19 sp.) was the most diverse habitat, followed by riparian environments (16 sp.) and swamps (9 sp.; Table 1). A medium-low similarity was found in the composition of species between the riparian and the forest (15 sp.; I_j = 0.25), as well as between the swamps and the forest (11 sp.; I_j = 0.21), although the data indicated only a minimal similarity when comparing rivers and swamps (2 sp.; I_j = 0.04; Table 1). The only species that were found in all three habitats were *Agalychnis spurrelli* and *Rhinella horribilis*.

According to the IUCN conservation status, one species is categorized as Data Deficient (DD), 54 as Least Concern (LC), and eight in the various threatened categories. *Pristimantis altae* and *P. caryophyllaceus* are categorized as Near Threatened (NT); *Craugastor persimilis* as Vulnerable (VU); *Duellmanohyla uranochroa*, *Ecnomiohyla veraguensis*, *Gastrotheca cornuta,* and *Bolitoglossa alvaradoi* as Endangered

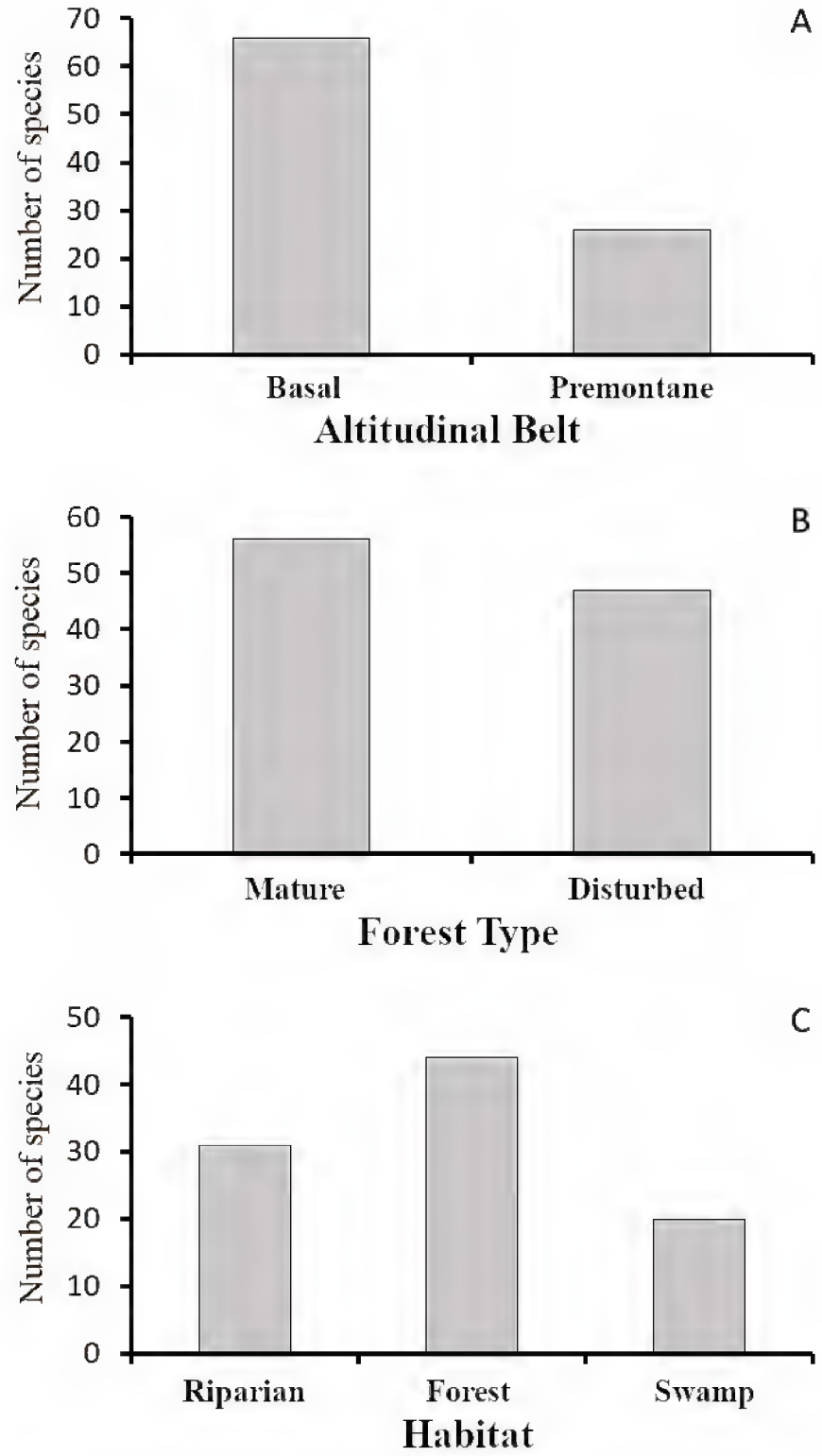

Fig. 3. Number of species registered according to the altitudinal belt (A), forest type (B), and habitat (C) in the study area.

(EN); and *Agalychnis lemur* as Critically Endangered (CR; Table 1). The species *Hyalinobatrachium dianae, D. amirae, C. sylviae, E. sukia*, *Ecnomiohyla bailarina,* and *O. berlini* remain uncategorized (Table 1).

Regarding the uncategorized species populations, few populations of *H. dianae* were observed in isolated streams within the basal mature forest. Populations with several individuals of *Diasporus amirae* were detected at the premontane belt. The species *C. sylviae* was found during 2011–2012 in only a few places within the forest. Generally, the adults were observed inside tree holes up to 3 m high. However, between 2012 and 2017, the species was more commonly observed reproducing throughout the year in VRP, near small artificial ponds (length 200 cm, width 150 cm, depth 50 cm) located within the forest. These ponds were created in 2012 by a project of the Veragua Foundation for the Rainforest Research "Veragua Foundation" (NGO) that aims to establish *in situ* breeding sites for the conservancy and study of the native amphibians. *Ecnomiohyla bailarina* and *E. sukia* were detected calling from the canopy in basal and premontane pristine forest. *Oedipina berlini*

Table 1. Checklist of amphibians of the Veragua Rainforest Eco Research and Adventure Park and its surroundings, with information on the voucher ID (UCR), IUCN status, altitudinal belt (basal [b] / premontane [p]), forest type (mature [M] / disturbed [D]), and habitat association (forest [F] / swamp [S] / riparian [R]).

Taxa	UCR	IUCN status	Altiudinal Belts	Forest Types	Habitats
Aromobatidae (1)					
Allobates talamancae (Cope, 1875)	21593	LC	b p	M D	F S
Bufonidae (4)					
Incilius coniferus (Cope, 1862)	21164	LC	b	M D	F S
Incilius melanochlorus (Cope, 1877)	21983	LC	b p	M	R F
Rhaebo haematiticus Cope, 1862	21139	LC	b p	M D	R F
Rhinella horribilis (Wiegmann, 1833)	21148	LC	b	D	R F S
Centrolenidae (10)					
Cochranella granulosa (Taylor, 1949)	23183	LC	b	M D	R
Espadarana prosoblepon (Boettger, 1892)		LC	b	D	R
Hyalinobatrachium chirripoi (Taylor, 1958)	21431	LC	b p	M D	R
Hyalinobatrachium dianae Kubicki, Salazar, and Puschendorf, 2015	22035		b	M	R
Hyalinobatrachium fleischmanni (Boettger, 1893)	23182	LC	b	M D	R
Hyalinobatrachium talamancae (Taylor, 1952)	21157	LC	b p	M	R
Hyalinobatrachium valerioi (Dunn, 1931)	21140	LC	b	M	R
Sachatamia albomaculata (Taylor, 1949)	21114	LC	b p	M D	R
Teratohyla pulverata (Peters, 1873)	21153	LC	b	M D	R
Teratohyla spinosa (Taylor, 1949)	21126	LC	b	M D	R
Craugastoridae (15)					
Craugastor brandsfordi (Cope, "1885," 1886)	21149	LC	b	D	F
Craugastor crassidigitus (Taylor, 1952)	21120	LC	b p	M D	R F
Craugastor fitzingeri (Schmidt, 1857)	21150	LC	b p	M D	F
Craugastor gollmeri (Peters, 1863)	22550	LC	b p	M	F
Craugastor megacephalus (Cope, 1875)		LC	b	M	F
Craugastor mimus (Taylor, 1955)	21414	LC	b	M D	F
Craugastor noblei (Barbour and Dunn, 1921)	21156	LC	b	M D	F
Craugastor persimilis (Barbour, 1926)	22529	VU	b	M	F
Craugastor polyptychus (Cope, 1886)	21121	LC	b p	M D	F
Craugastor talamancae (Dunn, 1931)		LC	b	D	R F
Pristimantis altae (Dunn, 1942)	21145	NT	b p	M D	R F
Pristimantis caryophyllaceus (Barbour, 1928)	21844	NT	p	M	F
Pristimantis cerasinus (Cope, 1875)	21127	LC	b p	M D	F
Pristimantis cruentus (Peters, 1873)	21170	LC	b p	M	R F
Pristimantis ridens (Cope, 1866)	21096	LC	b p	M D	R F
Dendrobatidae (4)					
Dendrobates auratus (Girard, 1855)	21128	LC	b	M D	F
Oophaga pumilio (Schmidt, 1857)	21106	LC	b p	M D	R F
Phyllobates lugubris (Schmidt, 1857)	21143	LC	b	M D	R F
Silverstoneia flotator (Dunn, 1931)	21986	LC	b p	M D	R F
Eleutherodactylidae (2)					
Diasporus diastema (Cope, 1875)	21415	LC	b p	M D	R F
Diasporus amirae Arias, Chaves, Salazar, Salazar-Zúñiga, and García-Rodríguez, 2019	22010		p	M	F

Table 1 (continued). Checklist of amphibians of the Veragua Rainforest Eco Research and Adventure Park and its surroundings, with information on the voucher ID (UCR), IUCN status, altitudinal belt (basal [b] / premontane [p]), forest type (mature [M] / disturbed [D]), and habitat association (forest [F] / swamp [S] / riparian [R]).

Taxa	UCR	IUCN status	Altiudinal Belts	Forest Types	Habitats
Hemiphractidae (1)					
Gastrotheca cornuta (Boulenger, 1898)	21017	EN	b p	M	R
Hylidae (23)					
Agalychnis callidryas (Cope, 1862)	21098	LC	b p	M D	F S
Agalychnis lemur (Boulenger, 1882)	21104	CR	b p	M D	S
Agalychnis saltator Taylor, 1955	21429	LC	b	M D	F S
Agalychnis spurrelli (Boulenger, 1913)	21119	LC	b	M D	R F S
Boana rufitela (Fouquette, 1961)		LC	b	M	S
Cruziohyla sylviae Gray, 2018	21422		b	M D	F S
Dendropsophus ebraccatus (Cope, 1886)	21103	LC	b	M D	S
Dendropsophus phlebodes (Stejneger, 1906)	21432	LC	b	D	S
Duellmanohyla rufioculis (Taylor, 1952)		LC	b p	M	R
Duellmanohyla uranochroa (Cope, 1875)	22002	EN	b p	M	R F
Ecnomiohyla bailarina Batista, Hertz, Mebert, Köhler, Lotzkat, Ponce, and Vesely, 2014	22287		b	M	F
Ecnomiohyla sukia Savage and Kubicki, 2010	22940		b p	M	F
Ecnomiohyla veraguensis Batista, Hertz, Mebert, Köhler, Lotzkat, Ponce, and Vesely, 2014	21941	EN	b p	M	F
Hyloscirtus palmeri (Boulenger, 1908)	21995	LC	b	M D	R
Isthmohyla lancasteri (Barbour, 1928)	21994	LC	b	M	R
Scinax boulengeri (Cope, 1887)		LC	b	D	S
Scinax elaeochroa (Cope, 1875)	21151	LC	b	D	F S
Smilisca manisorum (Taylor, 1954)		LC	b	D	S
Smilisca phaeota (Cope, 1862)	21113	LC	b	M D	S
Smilisca puma (Cope, 1885)		LC	b	D	S
Smilisca sordida (Peters, 1863)	21099	LC	b	M D	R
Tlalocohyla loquax (Gaige and Stuart, 1934)	21097	LC	b	M D	S
Leptodactylidae (2)					
Leptodactylus melanonotus (Hallowell, 1861)	21518	LC	b	D	F S
Leptodactylus savagei Heyer, 2005	20107	LC	b	M D	F S
Microhylidae (1)					
Hypopachus pictiventris (Cope, 1886)		LC	b	D	S F
Ranidae (2)					
Lithobates vaillanti (Brocchi, 1877)	21101	LC	b	D	R
Lithobates warszewitschii (Schmidt, 1857)	21102	LC	b	M D	R F
Plethodontidae (3)					
Bolitoglossa alvaradoi Taylor, 1952	22048	EN	b	M	F
Bolitoglossa colonnea (Dunn, 1924)	21178	LC	b p	M D	F
Oedipina berlini Kubicki, 2016	22882		b	D	F
Caeciliidae (1)					
Caecilia volcani Taylor, 1969		DD	b	D	F

Plate I. Photos in life of amphibians recorded in the sampling area: **(A)** *Allobates talamancae*; **(B)** *Incilius coniferus*; **(C)** *I. melanochlorus*; **(D)** *Rhaebo haematiticus*; **(E)** *Rhinella horribilis*; **(F)** *Cochranella granulosa*; **(G)** *Espadarana prosoblepon*; **(H)** *Hyalinobatrachium chirripoi*; (**I**) *H. dianae*; **(J)** *H. fleischmanni*; **(K)** *H. talamancae*; **(L)** *H. valerioi*; **(M)** *Sachatamia albomaculata*; **(N)** *Teratohyla pulverata*; and **(O)** *T. spinosa. Photos by Víctor Acosta-Chaves* (C, G, N)*; Javier Lobón-Rovira* (A, F, L, M, O)*; José Andrés Salazar-Zúñiga* (B, D, E, H, J, K)*; Andréi Solís* (I).

was observed once in the secondary basal forest, as an individual was on the leaf litter on one of the trails of the Veragua Rainforest Park at night.

Observations on the Threatened Species

Pristimantis altae (NT; Plate II-K) was seen and heard in mature and secondary forests (Table 1). At the basal belt, isolated males were recorded on riversides and inside the forest; nevertheless, at the premontane belt, groups of at least six calling males were registered, found very close to each other (2–3 m apart). At the premontane belt, *P. caryophyllaceus* (NT; Plate II-L) was commonly observed perched on leaves in the understory (100–150 cm high). On one occasion, a female was found in brooding position over a fully developed clutch with 26

Plate II. Photos in life of amphibians recorded in the sampling area: **(A)** *Craugastor brandsfordi;* **(B)** *C. crassidigitus*; **(C)** *C. fitzingeri*; **(D)** *C. gollmeri*; **(E)** *C. megacephalus*; **(F)** *C. mimus*; **(G)** *C. noblei*; **(H)** *C. persimilis*; **(I)** *C. polyptychus*; **(J)** *C. talamancae*; **(K)** *Pristimantis altae*; **(L)** *P. caryophyllaceus*; **(M)** *P. cerasinus*; **(N)** *P. cruentus*; **(O)** *P. ridens. Photos by Víctor Acosta-Chaves* (C, F)*; Javier Lobón-Rovira* (B, K, O)*; José Andrés Salazar-Zúñiga* (A, D, E, G–J, L–N).

eggs inside a partially rolled leaf at 1 m high. The female and her eggs were collected and placed in a plastic bag, and the next day all the eggs had hatched inside the bag. *Craugastor persimilis* (VU; Plate II-H) was observed several times during the plot survey, hidden in the leaf litter in the premontane belt.

Duellmanohyla uranochroa (EN; Plate IV-E) was detected in a few streams in pristine forest (Table 1). Males were observed calling from the streamside vegetation. Also, a male chorus was heard inside the forest at a distance of at least 100 m from the nearest stream. Some of these individuals were located in between the aerial roots of a walking palm (*Socratea exorrhiza*). *Ecnomiohyla veraguensis* (EN; Plate IV-H) was observed once calling from the canopy in the basal mature forest. *Gastrotheca cornuta* (EN; Plate III-G) was uncommon in the survey samplings. Only two populations are known in the study area; one of them was last reported in 1996

Plate III. Photos in life of amphibians recorded in the sampling area (unless otherwise specified, all photographs refer to specimens detected in Veragua): **(A)** *Dendrobates auratus*; **(B)** *Oophaga pumilio*; **(C)** *Phyllobates lugubris*; **(D)** *Silverstoneia flotator*; **(E)** *Diasporus diastema*; **(F)** *Diasporus amirae*; **(G)** *Gastrotheca cornuta* (Veraguas, Panama); **(H)** *Agalychnis callidryas*; **(I)** *A. lemur*; **(J)** *A. saltator*; **(K)** *A. spurrelli*; **(L)** *Boana rufitela. Photos by Abel Batista* (G)*; Javier Lobón-Rovira* (A–C, E, H, I, K, L)*; José Andrés Salazar-Zúñiga* (D, F, J).

at 200 m asl in the Victoria river basin (Solorzano et al. 1998), and the subsequent record was published 16 years later, in the streamside vegetation in a deep canyon of the Zent River at 550 m asl (Salazar 2015).

Three populations of the Critically Endangered *Agalychnis lemur* (Plate III-I) were observed throughout Veragua. One of the populations was located in a pond (width 35 m) in a mature premontane forest, where many males were observed calling from the vegetation at 50–150 cm high. The other two populations were found in secondary forest at the basal belt, including a population that is on the border of the VRP (Table 1). Outside the reserve, this species was observed in small ponds and flooding banks next to a wood extraction road. Thus, given this immediate threat, small artificial ponds (length 200 cm, width 150 cm, depth 50 cm) were created by the Veragua Foundation during 2015 to protect this population. As of 2016, it was easier to observe individuals throughout the year during high-humidity nights near these reproductive sites.

Discussion

With 215 species, Costa Rica is the 19th richest country in the world for amphibians, and exhibits the highest richness per unit area in Middle America (Kubicki 2008; Frost 2019). In this region, amphibian species density seems to be greater towards the South, specifically in Costa Rica and Panama (Campbell 1999). The results presented here show that Veragua exhibits the highest known species richness among Middle American lowland evergreen forests. With a notable anuran representation of 64 species in 51 km^2 surveyed (Table 1; Plates I–V), these

Plate IV. Photos in life of amphibians recorded in the sampling area (unless otherwise specified, all photographs refer to specimens detected in Veragua): **(A)** *Cruziohyla sylviae*; **(B)** *Dendropsophus ebraccatus*; **(C)** *D. phlebodes*; **(D)** *Duellmanohyla rufioculis*; **(E)** *D. uranochroa*; **(F)** *Ecnomiohyla bailarina* (Darien, Panama); **(G)** *E. sukia*; **(H)** *E. veraguensis* (Veraguas, Panama); **(I)** *Hyloscirtus palmeri*; **(J)** *Isthmohyla lancasteri*; **(K)** *Scinax boulengeri*; **(L)** *S. elaeochroa*; **(M)** *Smilisca manisorum*; **(N)** *S. phaeota*; **(O)** *S. puma*; **(P)** *S. sordida*; **(Q)** *Tlalocohyla loquax*. *Photos by Víctor Acosta-Chaves* (M); *Abel Batista* (F); *Edwin Gómez-Méndez* (O); *Daniel Hernández* (C); *Andreas Hertz* (H); *Javier Lobón-Rovira* (A, B, J, N); *José Andrés Salazar-Zúñiga* (D, E, G, I, K, L, P, Q).

Plate V. Photos in life of amphibians recorded in the sampling area: **(A)** *Leptodactylus melanonotus*; **(B)** *L. savagei*; **(C)** *Hypopachus pictiventris*; **(D)** *Lithobates vaillanti*; **(E)** *L. warszewitschii*; **(F)** *Bolitoglossa alvaradoi*; **(G)** *B. colonnea*; **(H)** *Oedipina berlini*; **(I)** *Caecilia volcani. Photos by Víctor Acosta-Chaves* (C, D, F); *Esmeralda Arévalo* (I); *Javier Lobón-Rovira* (E); *José Andrés Salazar-Zúñiga* (A, B, G, H).

surveys reveal one of the highest numbers of amphibian species reported per unit area in the Neotropics (Savage 2002; Boza-Oviedo et al. 2012; Barrio-Amorós et al. 2011; Hertz et al. 2012; Arias and Bolaños 2014; Ferreira et al. 2017).

In comparison with the most important diversity hot spots from South America, the richest region of amphibian species worldwide (Ron et al. 2018; Frost 2019), Veragua is also one of the most diverse localities in the Neotropics with 68 species. Only certain sites across the Amazon lowlands exhibit a greater richness of amphibians than these Veragua sites (Barrio-Amorós et al. 2011; Ferreira et al. 2017). For example, amphibian richness in Brazil ranged from 18 species (Alter do Chão, Pará) to as many as 78 species along a small section of the Juruá river (Zimmermann and Rodrigues 1990; Lima 2008; Queiroz et al. 2011; Pereira-Júnior et al. 2013; Araújo and Costa-Campos 2014; Alves-Binicio and Dias-Lima 2017; Ferreira et al. 2017; Lima et al. 2017), with the extreme exception of 109 amphibian species in the middle of the Xingu River (Vaz-Silvia et al. 2015; Ferreira et al. 2017). In Peru, the most diverse sites are in Bajo Río Llullapichis (74 sp.; Schluter et al. 2004), Parque Nacional Manu (68 sp.; Morales and Mcdiarmid 1996), and Cuzco Amazónico (64 sp.; Duellman 2005; Barrio-Amorós et al. 2011). In Colombia, the highest diversity was found in Leticia 97 species (Lynch 2005), and the two most important inventories reported in Ecuador are from the village of Santa Cecilia (87 sp.; Duellman 1978) and Parque Nacional Yasuní (135 sp.), currently the most diverse amphibian site in the world (Ron et al. 2018).

In Costa Rica, the amphibian richness is concentrated in the southern lowlands of the country and in the northeastern Atlantic versant (Campbell 1999; McDiarmid and Savage 2005; Santos-Barrera et al. 2008). Compared to the three other major inventories in these areas, Veragua is more species-rich than either the South Pacific locality of Rincón (47 sp., Anura [42]/ Caudata [4]/Gymnophiona [1]; McDiarmid and Savage 2005), the Atlantic versant sites of La Selva Biological Station (52 sp., 47/3/1; Guyer and Donnelly 2005), or Guayacán (66 sp., 58/6/2; Kubicki 2008). Other important inventories were reported in a transitional wet-dry forest in the locality of Carara (39 sp.; Laurencio and Malone 2009), and among the richest sites in dry forests is Finca Taboba, at the northern edge of the country (21 sp.; Campbell 1999).

The low diversity of salamanders found in Veragua could be due to fact that the sampling area was below 1,100 m asl, and that only one monitoring was conducted per year in the premontane belt. It is also possible that the sampling method was not inclusive enough to cover a broader diversity in the basal belt. The number of frog and

salamander species distributed along specific elevations in Middle America follows a pattern previously noted in Guatemala and Belize, i.e., a moderate number of species in the lowlands that progressively increases as it reaches moderate or intermediate elevations, and then declines precipitously at higher elevations (Campbell and Vannini 1989; Wells 2007). Salamanders partly show this pattern as they exhibit a more dramatic increase in species in the highlands (Campbell 1999; Wells 2007). We presume that some other species, such as *Bolitoglossa striatula, Nototriton matama, Oedipina carablanca,* and *Oedipina gracilis,* which occur in the Atlantic Versant at a similar altitudinal belt and close to the Talamanca mountain range (Savage 2002; Kubicki 2008; Leenders 2016), could also occur in Veragua. Among caecilids, only *Caecilia volcani* was found. The apparent low diversity in this group is probably caused by its fossorial habits (Peloso 2010; Ferreira et al. 2017) which undermine effective sampling. We think that at least one common caecilid species in the Atlantic Versant (*Gymnophis multiplicate*) could be present in Veragua (Leenders 2016).

In this study, the basal belt was found to be more diverse than the premontane (Fig. 3; Table 1). This is a generalized pattern of distribution among anurans (Savage 2002) and should account for the vast representation of frogs and toads in this study, which represent 94% of the total amphibian species. The latter species distribution is similar to that of the wet slopes of the Andes, the region with the highest diversity of anuran species in the world (Duellman 1999b; Wells 2007). The higher number of anuran species in old mature forests compared with disturbed areas might be explained by the presence of more microhabitats in pristine environments (Table 1; Savage 2002; Acosta-Chaves et al. 2015). Nevertheless, one of the main factors shown to influence high local and regional diversity is the variety of habitats with numerous vegetation types, ranging from forests to open grasslands, that occur side-by-side in the landscape, each of them harboring a different array of species (Colli et al. 2002; Nogueira et al. 2009; Lopes-Santos et al. 2014).

The greatest species diversity and the highest level of endemism for amphibians in Middle America occur along the windward mesic slopes of major mountain ranges between elevations of 800 and 2,800 m asl, which in Costa Rica include the Guanacaste, Tilarán, and Talamanca mountain ranges (Campbell 1999). The Talamanca mountain range is recognized as a site of speciation and a dispersion center for several species with a high degree of endemism (Arias and Bolaños 2014). Among amphibians and reptiles, 27% of the species in Costa Rica are endemic to this region (Campbell 1999; Savage 2002; Chaves et al. 2009; Streicher et al. 2009; Boza-Oviedo et al. 2012; Arias and Bolaños 2014). In this study, 8.7% of the amphibians are endemic to the Atlantic Versant of Costa Rica (Campbell 1999; Leenders 2016; Frost 2019), including species of the genera *Duellmanohyla* and *Isthmohyla*, which are endemic to Middle America (Faivovich et al. 2018).

A high number of species was found along the forest and the riparian habitats (Fig. 3; Table 1). This association with a type of forest might be due to the great variety of microhabitats found throughout these environments that result from irregular topography (Wells 2007; Kubicki 2008). Leaf litter is an important habitat for anurans, especially among species with terrestrial reproduction (although it is not restricted to them; Wells 2007). The high moisture levels found in the forest floor allow terrestrial species to forage and call during either the day or night (Wells 2007). The species richness of leaf litter frogs and toads is positively correlated with the number of wet months and the litter mass depth (Wells 2007; Whitfield et al. 2007).

The distribution along the riparian habitats was found to be non-uniform, as it could rely on vegetation coverage and the physical characteristics of the environment. The high number of amphibian species found along riparian habitats in this study could be due to the numerous springs, streams, and torrents found throughout the sampling area (Fig. 1), which generate several microhabitats along this environment (McDiarmid and Savage 2005; Kubicki 2007; SINAC 2018). Previous studies found a similar distribution pattern in Guayacán, where 35% of the species are associated with lotic environments (Kubicki 2008), while glass frogs represent more than 16% of the amphibian diversity in La Selva (Guyer and Donnelly 2005) and Rincón (McDiarmid and Savage 2005). In the mountainous regions of Middle America, the permanent or temporary ponds required for amphibian breeding are often scarce (Wells 2007). This pattern is also seen at Veragua and Guayacán, where the highly irregular topography of these localities causes permanent ponds to be a much more limited resource for reproduction (Kubicki 2008). Nevertheless, pond-breeders account for a notable representation of anuran species in Veragua (32, 4%) and Guayacán (30%; Kubicki 2008).

The species accumulation curve reached an asymptote, meaning that the sampling effort to detect species produced a number near the maximum expected value (Fig. 2). Nevertheless, there may be some cryptic species groups with high variation, and this fact may obscure the estimates given here, as different species could be hidden under a single name (Funk et al. 2012; Alves-Binicio and Dias-Lima 2017). However, the clarification of such unknown diversity requires further integrative taxonomic studies. Likewise, we suggest a larger survey effort in the premontane belt, since the difficult access to sampling areas did not allow for a continuous sampling.

Comments on Threatened Species

This study registered *P. altae* (NT), which has been previously reported in very few places on the Atlantic Slope of Costa Rica and northwestern Panama (Leenders 2016). Overall, there is only limited information about

its natural history, population trends, and conservation needs (Leenders 2016). Historically, *P. altae* has been associated with undisturbed areas (Savage 2002; Pounds et al. 2008a). Even though this species was observed in mature forests, it was also commonly detected close to streams within secondary forests. According to Savage (2002), this species is mute; however, during high humidity dark nights it is common to hear the species emitting a short two note call "clock-clock," similar to the sound that two glass marbles emit when they hit each other twice very rapidly. In basal secondary forests, isolated males were heard calling in the forest. However, on the premontane belt, this species is more abundant, and several males were heard calling at a close distance from each other. Unfortunately, the calls are emitted sporadically, and have not yet been recorded.

In this study, *P. caryophyllaceus* (NT) was one of the most common frogs in the mature premontane belt. During the mid-1980s, when many populations in Costa Rica declined (Leenders 2016), *P. caryophyllaceus* disappeared from most lowlands; however, it persisted at higher elevations (Leenders 2016). This pattern is rare among Neotropical anurans, considering that more pronounced declines generally occur at mid- and high elevations; in Panama, populations declined dramatically in some highlands, but in Costa Rica they seem to be recovering in areas above 800 m asl (Savage 2002; Pounds et al. 2008b; Leenders 2016). A female was found inside a rolled leaf at 100 cm above the forest floor attending a mass of 29 eggs. This same behavior was previously reported in Panamanian populations by Myers (1969). Recent research showed that *Craugastor persimilis* (VU) is susceptible to habitat fragmentation and it is often absent in open pasture lands and pineapple plantations (Bolaños et al. 2008). This observation is consistent with the observations reported here, as this species was only observed in the mature premontane forest.

Duellmanohyla uranochroa (EN) was a historically common species across humid lowland and mountain forests (Savage 2002). However, it has declined precipitously since the late 1980s. By 2002, *D. uranochroa* had experienced a significant decline across several populations in Costa Rica (Duellman 2001; Savage 2002; Leenders 2016; IUCN 2019). However, since 2007 some populations have reappeared in Monteverde, the Matama mountains, and Tuis de Turrialba (NatureServe and IUCN 2013), as well as in western Panama (Hertz et al. 2012). In this monitoring effort, populations were observed at the premontane and basal belt of the mature forest, sometimes close to riparian environments. Generally, males were found on the forest floor or on walking palm roots, and up to 2 m high. Similar behaviors have been reported in other populations of this species (Duellman 2001; Savage 2002; NatureServe and IUCN 2013).

Before this report, *Ecnomiohyla veraguensis* was only known from two small Panamanian populations in Santa Fé National Park, where it is highly threatened by ongoing habitat modification due to forest clearance for agriculture and open pit mining (IUCN SSC Amphibian Specialist Group 2019). *Ecnomiohyla veraguensis* is differentiated here from *E. miliaria,* another congener from the Caribbean foothills, based on the presence of scalloped fleshy fringes and the absence of heel tubercles in the former (Batista et al. 2014); from *E. bailarina,* considering that *E. veraguensis* has a finely tuberculate dorsum (strongly tuberculate in *E. bailarina*) with scattered minute keratin tipped tubercles on the posterior part of the body and 6–8 widely spaced, keratinized black spines bordering the outer side of the thumb (two clusters of numerous, small nuptial spines in *E. bailarina;* Batista et al. 2014). The most similar species to *E. veraguensis* is *E. sukia*; however, the latter lacks nuptial spines in adult males (Batista et al. 2014).

Gastrotheca cornuta (EN) is considered a rare species in Colombia and Costa Rica, while it has declined in Ecuador and Panama (Coloma et al. 2008; AmphibiaWeb 2009). In Costa Rica, this species is known from only three localities in the Limón Province (Coloma et al. 2008). The first specimen was collected during 1984 in the northwest of Nimaso peak in the Talamanca Mountain range at 700 m asl (Solorzano et al. 1998; Savage 2002). The other two localities were reported in Veragua, also at basal mature forests (Solorzano et al. 1998; Salazar 2015).

Bolitoglossa alvaradoi (EN) was only observed once in the mature forest. This endemic species has only been reported in undisturbed areas and it is considered endangered because its extent of occurrence is less than 5,000 km^2 (Bolaños et al. 2008). This salamander is a rare species, mostly due to its secretive arboreal habitats (Bolaños et al. 2008). In the current survey, this species was found during the day near a small stream on a leaf at 100 cm. Some other studies reported individuals inside bromeliads and leaf axils during the day (Wake 1987; Savage 2002).

Agalychnis lemur (CR) occurs in Costa Rica, Panama, and marginally in Colombia (Solís et al. 2008). It inhabits basal and premontane humid forests and has been historically associated with pristine areas (Duellman 2001; Savage 2002). This species has always been fairly uncommon throughout its range; however, it was listed as Critically Endangered because of ongoing drastic population declines, estimated to be more than 80% over a ten-year period (Solís et al. 2008). This survey found three separate natural breeding populations in the study area. One of these populations was already reported in Costa Rica and was considered the only remnant wild breeding population (Solís et al. 2008). Another small population was reported in Guayacán (Kubicki 2008; Solís et al. 2008). All other previously known Costa Rican populations of this species have disappeared, including those in Monteverde, San Ramón, Braulio Carrillo, and Tapantí (Solís et al. 2008).

The main threats reported for *A. lemur* are habitat

destruction and chytridiomycosis (Solís et al. 2008). In one of the reported populations in this study, Whitfield et al. (2017) found a low infection prevalence (<10%, n = 20) of *Batrachochytrium dendrobatidis* (*Bd*) and a low infection intensity among infected individuals. Some studies demonstrated that highly *Bd*-susceptible amphibians persist in environments hostile to *Bd*, even when *Bd* is still present (Puschendorf et al. 2011). The samplings reported here never registered a sick animal. Nonetheless, in some places where it was common to see the species during the sampling surveys, *A. lemur* had disappeared after the intensification of wood extraction during 2013. *Agalychnis lemur* appears to be highly susceptible to habitat loss, and the lack of natural reproductive sites in the forest promotes the use of the flooding banks or small ponds at the forest edge (JASZ, pers. obs.), a condition that we consider makes this species extremely vulnerable to habitat fragmentation.

This study shows that the threatened species reported here are associated with mature forest. These species may be sensitive to changes in their environment and might therefore exhibit a low tolerance to human impact (Dixo and Martins 2008; Lopes-Santos et al. 2018). The main biodiversity threats observed while conducting this study were: 1. Habitat destruction (legal or illegal) due to population growth, pastures, and extraction labors for wood and stone; 2. Monocultures of extensive plantations (e.g., by banana and pineapple corporations in the nearby lowlands), that also create substantial soil erosion and use numerous agrochemicals to maintain the crops, producing substantial amounts of pollution residues (Castillo et al. 1997; Castillo and Ruepert 2001; Sasa et al. 2010); 3. Illegal wildlife extraction; 4. Little control by the responsible authorities; and 5. Low levels of environmental education.

Conclusions

This survey shows that Veragua is a high priority conservation area with 11.7% of its amphibian diversity under the IUCN threatened categories, out of which five species are cataloged as Endangered or Critically Endangered (Table 1; IUCN 2019). In addition, this study reports *E. veraguensis* in Costa Rica for the first time and represents the only locality known for *E. bailarina* (Kubicki and Salazar 2015). The diversity analysis reveals one of the most important amphibian hot spots in the Neotropics, with evidence of recent sightings of several species after concerning declines (like those of *Duellmanohyla uranochroa* and *Agalychnis lemur*), and contrasts with the decimated diversity in several other important locations in Costa Rica (e.g., La Selva, Rincón de Osa, Cerro Chompipe, Monteverde, Cerro de la Muerte, Tapanti, Volcán Cacao, Palmar Norte, and Las Tablas) that have declined or disappeared since the late 1980s (Whitfield et al. 2007; Sasa et al. 2010; Ryan et al. 2015). Based on these findings, we suggest a long-term monitoring of the biodiversity in order to have control over population fluctuations, and we highly recommend natural history and behavioral studies to improve conservation actions across this biodiversity hot spot. According to the international conservation agreements, as well as Costa Rica's laws and executive decrees, the information provided in this article should help to protect the area from invasive activities that may negatively affect the biodiversity or major river basins (Sasa et al. 2010).

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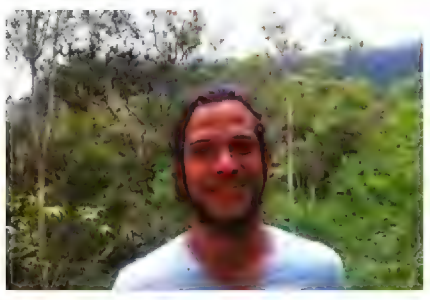

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